

**Modelling individual variability
in a social spider colony (*Stegodyphus dumicola*: Eresidae)
in relation to food abundance and its allocation**

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Modelling individual variability in a social spider colony (*Stegodyphus dumicola*: Eresidae) in relation to food abundance and its allocation. -

An individual-oriented model is developed to describe the population dynamics of social spiders. As a consequence of group living, individuals affect each other's behaviour, development and reproduction. As an example, the spider *Stegodyphus dumicola* (Eresidae) is investigated. The survival and development of individual spiders and of the colony depends considerably on food availability. The model demonstrates that complex behavioural functions, such as competition over food, can lead to distinct individual variances in body-masses of spiders at all life stages. The model results confirm field observations about the association between contest competition and individual variability. Colonies in which individual variability in body-masses was high due to contest competition survived longer in periods of food scarcity than colonies with scramble competition where the variability was lower.

Key-words: individual-oriented model - social spiders - contest competition - scramble competition - individual variability - colony survival - *Stegodyphus*.

INTRODUCTION

Non-territorial permanently social spiders share their food and may compete for this resource (WARD & ENDERS 1985; VOLLRATH 1986; RYPSTRA 1993; WILLEY & JACKSON 1993). A dominance hierarchy in the group can lead to unequal sharing, with some spiders receiving more than others (RYPSTRA 1993). Alternatively, food may tend to be evenly or randomly distributed among group members. This could be the case with small prey that individual spiders appropriate for themselves, or with solitary-living conspecifics.

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Members of social groups of *Stegodyphus dumicola* Pocock, 1898 (Eresidae) in Namibia differ considerably in size (HENSCHEL *et al.* 1995). From this variation, which occurs within the same cohort and sex, one can deduce that individuals differ in development rate. Ultimately, such differences should be reflected in variable reproductive success (SEIBT & WICKLER 1988; HENSCHEL *et al.* 1995; see also RYPSTRA 1993). This variability is probably a consequence of competition among group members over food.

We focus on two questions: (1) how does the degree of competition for food affect colony development and (2) how does variance in individual fitness affect the survival of colonies. We developed an individual-oriented model which allows the investigation by simulation of colonies over many generations under specified conditions. We base the model on life-history parameters reported for different *Stegodyphus* species (SEIBT & WICKLER 1988; SCHNEIDER 1992; WARD & LUBIN 1993) with emphasis on *S. dumicola* in Namibia (HENSCHEL *et al.* 1995; HENSCHEL 1996).

In order to investigate the influence of competition over food on colony development, we use two contrasting scenarios based on rules of two extreme types of intraspecific competition – "contest" and "scramble" (NICHOLSON 1954). Contest competition, in which dominant individuals feed before others, leads to a predictable and biased allocation of resources. A stable, linear social hierarchy is an extreme of this case (e.g., HENSCHEL & TILSON 1988). By contrast, food allocation is unpredictable in scramble competition where any individual can obtain much food from captured prey at one occasion and little on another occasion. This may depend on the time of arrival of an individual at prey, the availability and quality of vacant positions at prey that it can occupy, and other (stochastic) factors. Individuals in scramble competition do not displace each other, but compete by feeding, thus reducing the amount left for others.

The current report concerns the first step of a model being developed to examine factors involved in the evolution and maintenance of sociality in spiders. For the present, we focus on the influence of food allocation and leave aside other possible factors, such as predation risk, emigration and interactions between colonies, that may affect the development of a particular colony. We limited the growth and longevity of a colony only by food resources and concentrate on the relative differences caused by contest and scramble competition. This allows us to make a preliminary, qualitative assessment of the role of food availability and competition in spider sociality.

METHODS

Phenology and development

Stegodyphus dumicola is a 100–260 mg spider (adult female size) that occurs in colonies comprising a few to hundreds of individuals (SEIBT & WICKLER 1988), or it occurs solitarily when a female disperses alone (HENSCHEL 1993, 1996). Colony members share common retreats and build large capture webs to trap flying or

jumping insects. Captured prey includes small insects that one individual can consume alone as well as large insects that are shared. *Stegodyphus dumicola* has an annual life cycle with non-overlapping generations, except during the nursery period (Fig. 1). The overall secondary sex-ratio is female-biased (female proportion = 88%). As a consequence of variance in growth, females mature more asynchronously and often later than the males (Fig. 2; HENSCHEL *et al.* 1995). Adult males are short-lived and females that mature too late may have no opportunity to mate. HENSCHEL *et al.* (1995) suggested that the relative timing of reproduction by different females in a colony may determine the size and development rate of their offspring.

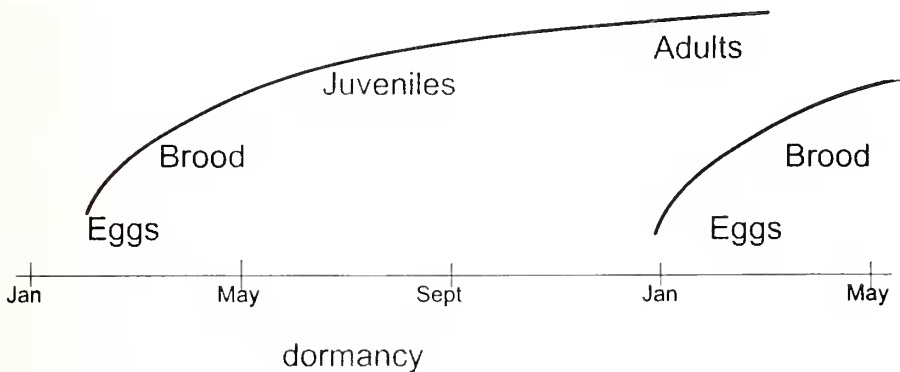


FIG. 1

Life cycle of *Stegodyphus dumicola* in Namibia, after HENSCHEL (1996). The first eggs are deposited in February; the brood hatches after two weeks; the nursery period precedes a dormancy period during June to August; the first adults mature in January.

The model-assumptions and rules

Parameters for the model are derived from field data (op. cit.) and are applied to the life cycle of the individuals within one colony. The time step is one day, as processes such as food allocation and reproduction have a resolution at this time scale. We distinguish between the main life stages: egg, brood, juvenile and adult. Rules for foraging, growth and reproduction are given for each of these stages. Indices are developed for individuals (i) and colonies (c). The parameters and their ranges are listed in Table 1. The values for parameters $f1$ – $f7$ were varied systematically in a limited range or had fixed values; their role was to yield realistic ranges of values for the dependent parameters in each equation.

FORAGING – We assume that spiders can eat every day. As larger colonies have larger capture webs (Henschel, unpubl.data), the daily food resource ("food $_c$ ") for the colony has a linear relationship with colony size as follows (eq. 1):

$$food_c = f1 * (f2 + f3 * (size + drand)) \quad (1)$$

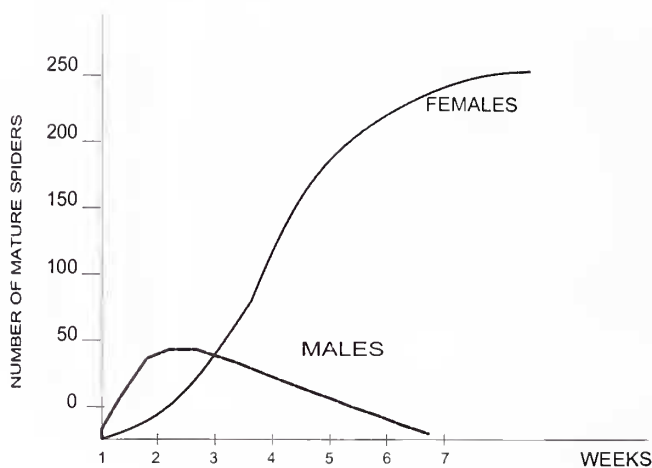


FIG. 2

Early maturation of males followed by asynchronous maturation of females of *Stegodyphus dumicola* (redrawn after HENSCHEL *et al.* 1995).

TABLE I
Model parameters

Parameter	Definition	Range	Dimension
f1	food level	1–6	
f2	parameter (eq. 1)	5	
f3	"	0.75	
size	colony size	0–700	
eat	daily food uptake	0–6.3	mg
need	daily need	0.75–6.3	mg
f4	parameter (eq. 4)	0.75–5.5	
f5	"	10–100	
f6	parameter (eq. 10)	0.5	
f7	parameter (eq. 10)	0.5	
resource	food resource		
energy metabolism		0.1–1.3	mg
eggnumber	size of clutch	10–100	

The parameter f1 represents the "food level", which is varied between different simulations. A food level of 1 is in accordance with a daily food availability in a range of 0.8 mg to 1.55 mg per spider. This is valid if the colony size is 100 and f2 = 5 and f3 = 0.75. Parameter f2 is the minimum amount of food, which is available for the colony independent of its size. The colony size is the number of juveniles and adults. Parameter f3 refers to the effect of the colony size on the daily food resource

food_c. The daily stochasticity of this relationship is expressed by means of the random function "drand", returning values from 0 to 1.

The food uptake ("eat_i") by an individual spider (i) is determined by the amount of food required ("need_i"), limited by the amount available at the time this individual feeds ("resource_i"). The individual takes the amount of food it needs or, if the resource available to the individual is smaller than the amount needed, it takes this resource (eq. 2):

$$eat_i = \text{minimum}(\text{resource}_i, \text{need}_i) \quad (2)$$

The food obtained by an individual depends on the type of food allocation, based on two rules of competition. The first is "contest" or hierarchical competition, with larger spiders having priority of access to food and receiving more food than small ones (RYPSTRA 1993; M. Whitehouse, pers. comm.). In this case, the individual resource for the largest spider ("resource₁") is the daily food resource ("food_c", see eq. 1). In the corresponding model procedure, the dominant (largest) individual has first choice of food, followed by others successively down the body-mass hierarchy until no food is left. In this way, the resource available to spider (i) depends on the food consumed by the spider that preceded it (eq. 3):

$$\text{resource}_i = \text{resource}_{i-1} - \text{eat}_{i-1} \quad (3)$$

The need of a spider depends on its body-mass ("mass_i") (ANDERSON 1970). Since little is known about the actual relationship for *S. dimicola*, we approximate this with eq. 4:

$$\text{need}_i = f4 + \frac{\text{mass}_i}{f5} * \text{drand} \quad (4)$$

Parameter f4 is the part of the individual need which is independent of the body-mass. The second part depends on the body-mass ("mass_i") and is varied by the random function "drand". For comparison with "contest" competition, we consider also "scramble" competition, in which the succession of access by individuals to food is changed randomly each day. Over long time periods, this random allocation of food tends to lead to an even distribution of food among colony members.

GROWTH – The growth of spiders is described by their change in mass ("Δ mass_i"), which is the result of feeding minus the energy required for metabolism and activities:

$$\Delta \text{mass}_i = \text{eat}_i - \text{energy}_i \quad (5)$$

An individual died of starvation if its mass declined to <50% of a mass that it had attained previously.

REPRODUCTION – Rules for reproduction depend on maturation, fertilization and egg laying. Due to the different maturation rates of males and females (Fig. 2) the operational sex ratio at the beginning of the mating period can be male-biased

(HENSCHEL *et al.* 1995). Therefore, the probability of reaching maturity in the first week of January is assumed to be higher for a male than for a female (eq. 6, 7). The actual date is described by the parameter "day".

$$P_{maturity_male}(day \leq 7) = \frac{day}{7} \quad (6)$$

$$P_{maturity_female}(day \leq 7) = 0,001 \quad (7)$$

Model females only mature at a mass >120 mg. After the first week, the probability of maturation per day increases for females:

$$P_{maturity_female}(day > 7) = 0,1 \quad (8)$$

All model males mature during the second week of January. All model females that mature in the first 14 days are fertilized. As males are available for reproduction only for a short period of several weeks (HENSCHEL *et al.* 1995), a rule for male mortality is introduced after the second week of January:

$$P_{mortality_male}(day > 14) = 0,1 \quad (9)$$

Due to the decreasing number of males, a further model rule expresses the fertilization of only the biggest virgin female every day after the first two weeks until all males disappear. The mortality of females increases after the beginning of April, as females are consumed by juveniles during this period.

Following the trend that larger spider females have a higher fecundity (SCHNEIDER 1992), our model spiders produced eggs according to their body-mass:

$$eggnumber_i = f6 * Weight_i^7 \quad (10)$$

Simulation runs

Colonies arbitrarily comprised 100 members upon entering the simulations. The development of individuals and colonies was tracked on a daily basis and an annual basis respectively. Records of the mass of individuals and of colony size were taken on 31 December, immediately prior to the first maturation. A colony goes extinct when none of the females is capable of reproducing. The time span to this condition is referred to as "colony life time". Mean colony life time for a certain food level was calculated over 100 simulations.

RESULTS

Contest competition over food leads to considerable individual variation in the development of different life stages (Fig. 3; CV = 22.5%). By contrast, scramble competition yielded significantly lower variances in mass (CV = 6.6%; $F_{151,218} = 37.8$, $P < 0.001$). Under conditions of food scarcity, none of the spiders reached maturity in colonies with scramble competition while some still succeeded in colonies with contest competition.

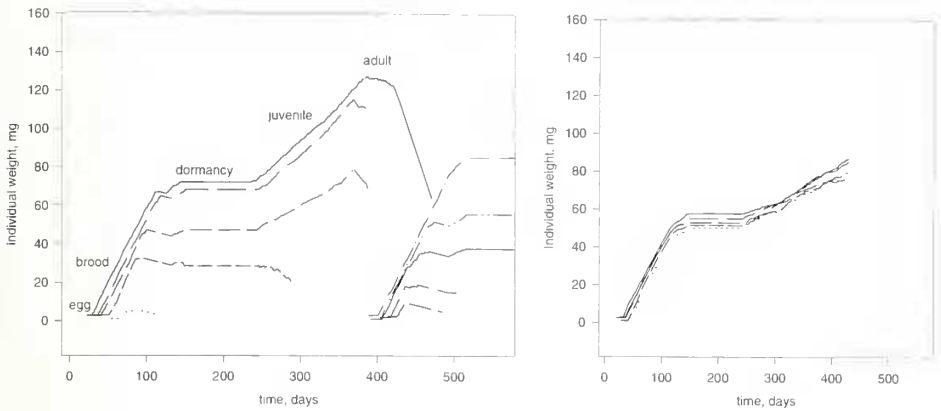


FIG. 3

Individual mass change over time of five randomly selected individuals in two successive generations in (a: left) a colony with contest competition and (b: right) a colony with scramble competition. The colony with scramble competition was extinct after one generation because no females reached maturity. The food level was 1.

Contest competition led to distinctively longer colony life times than did scramble competition (Fig. 4). Under conditions of food scarcity reproduction is possible only in a hierarchical colony with contest competition. In both conditions, mean colony life time correlated closely with the food level ($r_2 = 0.97$ and 0.93 for contest and scramble competition respectively, $P < 0.001$; $\log(y)$ - transformation). Therefore, mean colony life time increases exponentially with increasing food level. The slopes of the regression equations differed significantly ($t = 4.46$, $df = 15$, $P < 0.001$; test follows ZAR 1984), being steeper for contest competition. Even slight increases of the values of food level (f_1 in eq. 1) caused considerable increases in the life time of colonies with contest competition. By contrast, colonies with scramble competition required higher food levels for reproduction to occur within them. Large increases in food level were necessary to cause slight increases in the average colony life time.

How colony development is affected by food abundance was demonstrated by tracking colony size over successive years under relatively different food conditions in colonies with contest competition (Fig. 5). At low food levels, the colony size varied in the range between 15 to 150 members. A threshold in colony growth was evident when the food level increased from $f_1 = 4$ to $f_1 = 5$. Above this threshold, the probability of colony extinction is low. Since there is ample food, few if any spiders die of starvation. With many adults of both sexes present, demographic stochasticity is low.

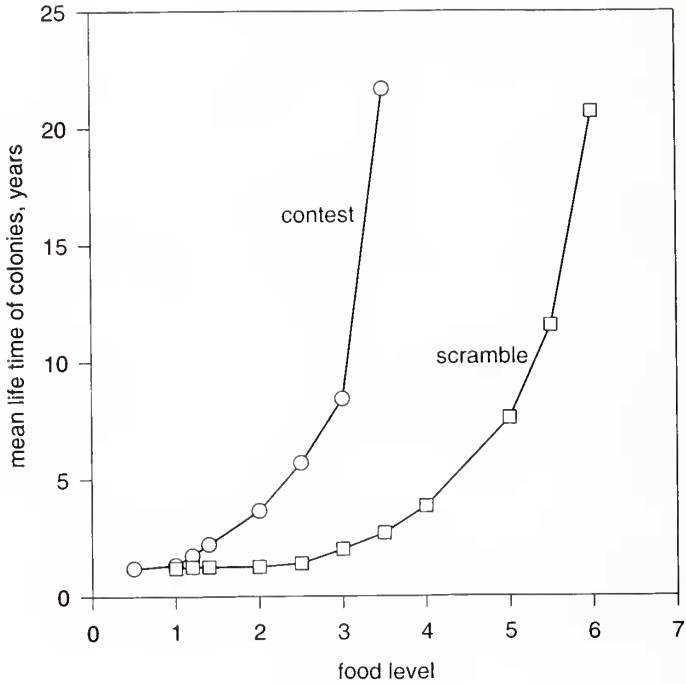


FIG. 4

Mean colony life time in over 100 simulations each of colonies with contest and scramble competition under various levels of food richness (FI variable in eq. 1).

DISCUSSION

The calculations incorporated into our model are very sensitive to the mathematical description of food availability and its allocation. Nevertheless, such modelling yields qualitative results that can point out the direction of the next step to be taken. In this initial approach, we have neglected limiting factors other than food shortage; therefore our model colonies could attain unrealistic sizes of up to thousands of spiders, whereas in reality *S. dumicola* colonies contain, at most, hundreds of individuals. Through our approach, it is possible to highlight the qualitative differences resulting from different food-sharing strategies.

Our model demonstrates that the unequal distribution of limited food among members of social groups appears to have a considerable effect on colony survival. In colonies with contest competition, juveniles that hatched early in the season maintained a life-long size advantage over juveniles that hatched later. Nevertheless, small spiders also took part in nest and web maintenance, and the overall food resources increased as a result of their work (see eq. 1). Thus, large spiders increase their

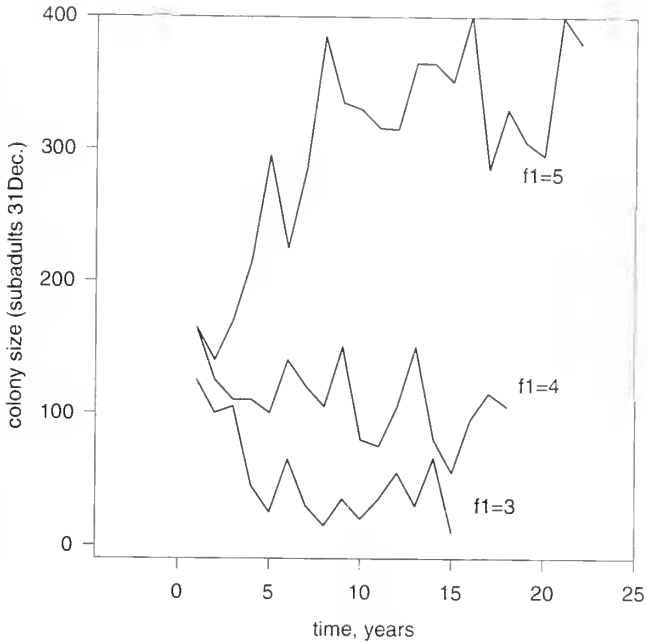


FIG. 5

Colony size development over years of colonies with contest competition at various levels of food richness. Colony size was calculated as the number of spiders present on 31 Dec., shortly before first maturation.

resource gain and, ultimately, the probability of survival, at the expense of the small spiders. The model calculations are consistent with observations that have suggested that individual variation is associated with contest competition (VOLLRATH 1986; RYPSTRA 1993; HENSCHER *et al.* 1995).

Contest competition leads to high variance in individual development rates within colonies, which has a stabilizing effect on the colony size and thereby prolongs the survival of the colony. In other words, the maintenance of a feeding hierarchy lowers the risk of colony extinction. We explain this in terms of the different allocation of limited resources. In colonies with contest competition, at least some dominant females are likely to reach the threshold size for reproduction (RYPSTRA 1993), except when food is extremely scarce. In colonies with scramble competition, however, even moderately high food supply may not suffice to get any of the similarly-sized females above the reproductive threshold in time to mate.

According to the results of our model, colonies with contest competition tend to grow consistently (with some fluctuations) at a high level of food richness (Fig. 5). A food coefficient of 5, which lies just above this growth threshold, is an average daily food availability of 4.0 to 7.75 mg per spider in a colony of 100 individuals.

Above this growth threshold, colonies are not expected to go extinct if there are no negative factors other than starvation and failure to reproduce.

We conclude that high variability among individuals reduces variability in colony size in successive generations and enhances colony survival when food richness is below a critical level. We intend to incorporate this conclusion into the next step of the model. This is to examine the effect of environmental stochasticity that causes within- and between-year variability in food availability. This should not only broaden our understanding of how food parameters affect colony size and survival, but also how they affect the fitness of individuals in the colony compared to that of solitary dispersers.

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